The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition

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Summary

The effect of deer on woodland vegetation is reviewed, focusing on processes that are likely to bring about changes in structure and composition. By browsing on tree seedlings, shrubs and climbers, deer tend to reduce stem densities, limit height growth and reduce foliage density, creating a more open understorey. Light penetration to the ground can be increased, providing more plant cover close to the ground surface. Using results from 13 studies in temperate woodlands, the effects of deer browsing on the species richness and diversity of trees were analysed using general linear models. The results show that deer tend to reduce the diversity of seedlings, and that the effect is greater at higher deer densities. Differences in susceptibility of tree species were evident, with some species being depleted by deer at all sites, whereas others declined in some sites but increased in others. The effects of deer on the amount and composition of regeneration appear to depend on site characteristics, including the light regime and composition of the ground vegetation. Although few studies of seed dispersal by ungulates (endozoochory) have been made in Britain, deer have been shown to be effective seed dispersers of a number of plant species. Plants with small hard seeds are most likely to survive digestion. Most of the species known to be dispersed in this way include grasses and small herbs. In view of the fact that dispersal mechanisms of many woodland species are not well understood, endozoochory may be more important than is generally realized.

Introduction

Following the removal of livestock in historical times, deer have become the main large herbivores in most lowland woodland ecosystems. The influence that they have on woodlands centres on the impact they have on the composition and structure of the vegetation. Most of the effects of deer on invertebrates and other fauna depend on vegetation changes. The best known effects are due to browsing on young trees, shrubs and herbs, which alters both structure and composition and may retard woodland successional development. Less well known are the effects on nutrient cycling and dispersal of seeds through the gut or on their coats. Recent studies in

Mediterranean ecosystems have identified a wide range of plant species (including many British species) that can survive passage through the gut of a deer. In view of the implications for fauna, the impact that deer have on woodlands is reviewed, focusing on the processes of browsing and seed dispersal and how these bring about changes in woodland structure and composition.

The impact of browsing

Changes in woodland structure

Changes in vegetation structure are perhaps the most conspicuous effect that deer have in woodlands. However, in spite of recent interest in developing methods to measure structure (Fuller and Henderson, 1992; Ferris-Kaan et al., 1998; K. Pommerening, 2001, personal communication), there is little quantitative information on overall structural changes in woodland created by varied browsing pressures. An account of these changes must therefore be descriptive or interpreted to some extent from measures such as seedling density or growth rate which are more readily quantifiable. Broadly, there are three main components to the structural changes caused by deer: browsing on seedlings, which limits stem density, browsing on leading shoots, which limits height growth, and browsing on side shoots and climbers, which reduces foliage density. Since deer tend to shift their feeding to side shoots as trees grow beyond reach, the relative importance of these effects depends to some extent on stand age and type.

The leading shoots and upper leaves are usually the most actively growing and nutritious parts of young trees and shrubs, and are actively selected by deer (Bryant and Kuropat, 1980; Harper, 1989). As a result, height growth is usually sharply reduced by browsing (Gill, 1992b; Gerber and Schmidt, 1996; Cermak, 1998). The loss of growth depends on the severity or frequency of browsing and may vary considerably between tree species, depending on the feeding selection by the deer or the ability of the trees to recover from damage (Eiberle, 1978; Roth, 1996; Gill et al., 2000). Comparisons of growth loss between fenced and unprotected plots shows that browsing

effectively delays height growth and in some cases also woodland succession. Tree seedlings have been reported to be kept to < 50 cm in height for as long as 25 years by browsing (Shaw, 1974) and some species will adopt a more squat form with denser foliage on the side branches. Besides trees, deer focus much of their feeding on shrubs and climbers, including bramble (Rubus fruticosus), honeysuckle (Lonicera periclymenum) and ivy (Hedera helix) (Holisova et al., 1992; Forde, 1989). Evergreen species constitute a large proportion of the available food biomass for deer in winter and therefore attract a lot of feeding. As a result the cover and height of climbers and shrubs are reduced (Putman et al., 1989; Morecroft et al., 2001). Plants that escape to grow above browsing height may have all foliage and side branches removed or depleted, producing plants which are tall but with reduced foliage and flowering potential (Pollard and Cooke, 1994; Martin and Daufresne, 1999).

In coppice woodlands, deer cause substantial damage to shoots that sprout after cutting, resulting in the death of the stool if damage is severe or repeated (Kay, 1993; Putman, 1994). When the shoots eventually grow beyond browsing height, the canopy may be shorter and more open (Cooke and Lakhani, 1996; Fuller, 2001). One outcome of the browsing pressure on trees, shrubs and climbers is an increase in light penetration, resulting in more vegetation at ground level (McInnes et al., 1992; Fuller, 2001).

Besides reducing height growth, browsing can also affect tree survival rates, resulting in substantially reduced seedling densities (Konig, 1976; Dzięciolowski, 1980; Putman et al., 1989; Healy, 1997). However, this is not always the case, and several studies have shown that seedling density is unaffected by browsing or reduced only in certain habitat types. In particular, seedling density appears to be affected less by browsing in openings, clearcuts or heavily thinned stands, than under unthinned stands (Tilghman, 1989; Ammer, 1996; Van Hees et al., 1996).

In studies where the fates of individual trees have been monitored, survival after browsing or clipping is age-dependent, with only the smallest or youngest seedlings being affected. Beyond a certain age, trees can often withstand repeated browsing (Gill, 1992b). This suggests that

browsing is directly responsible for the death of only very small or young seedlings.

In some cases, a lower survival rate or seedling density has been recorded *inside* enclosures (Dzięciolowski, 1980; Risenhoover and Maass, 1987; Welch *et al.*, 1992; Gill *et al.*, 2000; Harmer and Gill, 2000). These results, together with the fact that the effect of browsing on seedling density varies with stand type and light regime, indicate that the mortality of young trees may be affected as much or more by competition from other plants than browsing directly.

The strength of competition is likely to vary considerably with the type of vegetation and the effect that deer have on it. Since deer usually deplete shrubs and climbers and bring about an increase in grasses, their effect may be to reduce competition where the former are dominant and the converse where grasses are more abundant. Hamard and Ballon (1998), for example, recorded lower browsing rates and better growth on trees surrounded by climbers than on trees without them. However, by reducing height growth, browsing may increase the chance that young trees will be outgrown and killed by competing vegetation, whatever the composition. There are therefore a number of mechanisms involved which account for the change in tree seedling density. Trees may be killed directly by browsing; browsing may reduce competitive ability; and the intensity of competition from other vegetation may be either increased, unchanged or reduced, depending on its palatability to deer. Further research is required to determine the role and significance of competition on tree survival and on the vegetation in general.

Changes in tree and shrub species composition

Deer are selective feeders, and are often reported to browse some plant species more heavily or frequently than others (Gill, 1992a). Furthermore, tree species differ in susceptibility to damage (Eiberle, 1975; Gill, 1992b). As a result, browsing usually leads to a change in species composition, often within a few years after a change in browsing pressure (Putman *et al.*, 1989; Morecroft *et al.*, 2001). To assess the implications of this for woodland diversity, both species richness and species diversity were calculated from data presented in 13 studies involving assessments of the relative abundance of young trees or shrubs in both enclosed and unprotected plots. Species richness is defined simply as the number of species, N and diversity H' calculated from the Shannon index, $H' = -\Sigma p_i \ln p_i$ where p_i is the proportional abundance of species i, $p_i = n_i/N$ (Magurran, 1988). The value of H' increases both in relation to increasing richness and increasing evenness (decreasing variability) in abundance in a sample. The contribution of deer to tree species richness and diversity was examined by comparing fenced and unfenced plots, as well as by including deer density as a variable in a general linear model (Table 1; Figure 1). The models controlled for site differences by including site as a factor.

The results show that deer reduce both tree species richness as well as diversity. Where deer population density was also recorded, the results indicated a greater loss at higher densities. Although there was insufficient data for shrubs to be analysed in the same way, the results reported by several other authors (Kraus, 1987; Gerber and Schmidt, 1996; Martin and Daufresne, 1999) indicate that shrub diversity also declines at high deer densities.

It is nonetheless clear from these results that there are large differences between sites in tree seedling diversity, due to ecological conditions or to management history, and that deer tend to reduce diversity of a range of woodland types in proportion to increasing density. In some cases, the results from sites with low-density populations suggest that tree seedling diversity is slightly higher than where no deer occur at all (e.g. Healy, 1997). However, there are too few data to determine how general this response is at low densities.

In view of the fact that there are few examples where the effect of variation in deer density was recorded *within* each locality or woodland type, it was not possible to use this analysis to investigate interactions, namely to test whether deer have a greater effect on diversity in some woodland types or localities than others. However, it is clear that deer do not always have the same effect on vegetation composition. Distinctions can be made between tree species that are almost always depleted by browsing and those that decrease in some sites but increase in others

Table 1: Results of the general linear models to assess the effect of deer browsing on tree species richness (N) and diversity (H)

Model	F	d.f.	r^2	Explanatory variable			
				Name	F	d.f.	P
1 $N = 9.64 \pm L - 1.645d$	10.39	12,68	0.65	L	10.39	11	0.0001
				d	10.36	1	0.002
2 $H = 2.07 \pm L - 0.352d$	5.43	9,44	0.53	L	5.1	8	0.0002
				d	8.06	1	0.0068
3 $N_d = 2.2092 + 0.796N_0 \pm L - 0.165D$	10.6	6,15	0.81	N_0	47.9	1	0.0001
				L	1.9	4	0.1 (n.s.)
				D	4.9	1	0.02
4 $H_d = 1.1372 + 0.708H_0 \pm L - 0.0826D$	64.8	4,4	0.98	H_0	62.2	1	0.002
				L	70.9	2	0.001
				D	55.2	1	0.002

In models 1 and 2, richness and diversity were compared between paired exclosures and unfenced controls (d) after accounting for between-site variation (L). Models 3 and 4 test the effect of deer density (D deer/km^2) on richness (N_d) and diversity (H_d) after accounting for the effect of location (L). These models were based on a smaller sample where deer density had been recorded, and used the values of richness and diversity recorded in exclosures (N_0,H_0) as a covariate. Analyses were based on data for young trees only (<11 years old), obtained from 13 studies carried out in temperate woodland sites in both Europe and North America: Dzięçiolowski (1980); Kraus (1987); Tilghman (1989); Putman *et al.* (1989); Jones *et al.* (1993); Gerber and Schmidt (1996); Van Hees (1996); Ammer (1996); Healy (1997); Scrinzi *et al.* (1997); Langbein (1997); Luthardt and Bayer (1998), author's unpublished data. Shrub species were excluded from these analyses because the majority of authors did not report them.
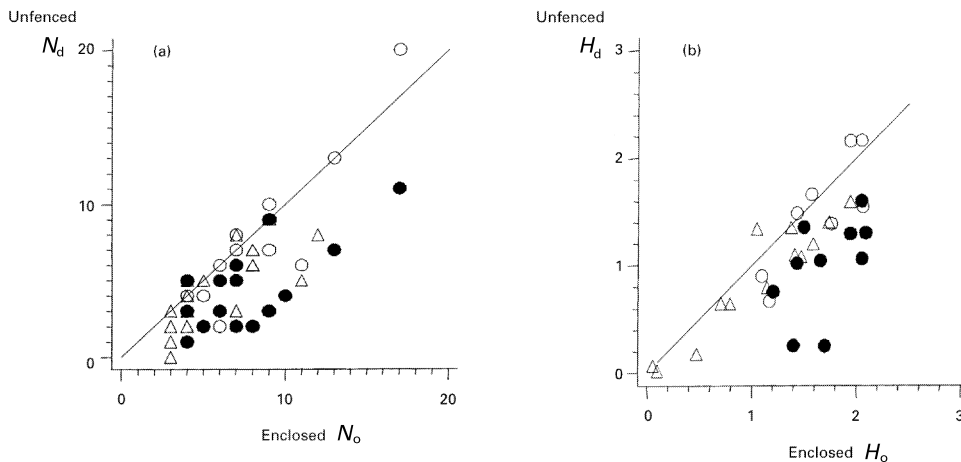

Figure 1. The effect of deer browsing pressure on tree species richness and diversity, assessed by comparison between fenced enclosures and unfenced controls: (a) the numbers of tree species; (b) tree species diversity. Data points are represented by open circles where deer density was below the median for a particular study or site and solid circles where it was above. Triangles represent sites where density was not recorded. The straight line marks the line of equal diversity. Data obtained from the same sources as used in Table 1.

Table 2: The effect of exclusion from deer on the relative abundance of some woody plant species

	Proportion of cases (%)		
	Abundance decreasing under browsing pressure	Abundance increasing under browsing pressure	Sample size (*n*)
Trees			
Oak *Quercus* sp.	100		24
Willow *Salix* sp.	100		10
Hornbeam *Carpinus betula*	100		8
Rowan *Sorbus aucuparia*	91		11
Ash *Fraxinus excelsior*	83		6
Aspen *Populus tremula*	83	17	6
Birch *Betula* sp.	70	30	10
Scots pine *Pinus sylvestris*	60	30	10
Field maple *Acer campestre*	60	40	5
Beech *Fagus sylvatica*	54	38	13
Shrubs and climbers			
Bramble *Rubus fruticosus*	92	8	12
Ivy *Hedera helix*	83	17	6
Hawthorn *Crataegus monogyna*	80	20	5
Honeysuckle *Lonicera periclymenum*	50	50	4

Data have been summarized from 10 European studies: Dzięçiolowski (1980), Kraus (1987), Putman *et al.* (1989), Gerber and Schmidt (1996), Van Hees (1996), Ammer (1996), Scrinzi *et al.* (1997), Langbein (1997), Luthardt and Bayer (1998), author's unpublished data. The sample sizes indicate the total number of sites where more than five individuals of the species was recorded. The sum of the two percentages is <100 where no change in abundance was recorded at one or more of the sites.

(Table 2). In lowland European conditions, oak, willow and hornbeam have been reported to decline in all cases, implying that reduction of at least these three species is a predictable outcome. In contrast, species such as beech and birch can occasionally increase. There is likely to be a variety of reasons why browsing may not create a consistent change in species composition. First, differences in diet exist between deer species, and feeding preferences depend on the composition of the vegetation (Danell and Ericson, 1986; Eiberle and Bucher, 1989). Consumption of plants of low-medium preference, for example, would be very dependent on the abundance of other food items. As a result, some differences in impact would be expected on the basis of the deer and vegetation species alone. Secondly, the ability of tree species to remain competitive would change with site characteristics: species would be expected to cope best with browsing when the moisture, light and nutrient regimes are close to optimal.

The implications of seed consumption and dispersal

Fruits and seeds are readily eaten by deer and other ungulates and may form a substantial part of their diet, particularly in autumn when many species are fruiting (Jackson, 1977; Holisova *et al.*, 1984; Tixier and Duncan, 1996). Seeds may also be eaten inadvertently, when other plant parts are being ingested. Ungulates are known to act as dispersal agents for a number of plant species by passing seeds through their gut (endozoochory), carrying them on their coats, or between their hooves (epizoochory), or simply spitting out seeds after mastication or rumination (Janzen, 1984; Bodmer, 1991). Factors that promote seed dispersal will increase access to germination sites and therefore increase population size. Conversely, if consumption of a plant species' seed normally results in destruction, then dispersal will be limited and populations of that species could be depleted (Olff and Ritchie, 1998). By influencing dispersal in these ways,

deer may be having a powerful selective influence on woodland vegetation, promoting some species while hampering others. However, seed dispersal by deer and other ungulates has not yet been widely studied in British conditions, although recent investigations elsewhere in Europe suggest that it may be important (Malo and Suarez, 1995).

Characteristics of endo- and epizoochorous species

The size and hardness of seeds are important qualities that affect viability after ingestion by herbivores. Large seeds, such as acorns or beech mast, are abraded and crushed by the grinding action of the teeth. To escape mastication, seeds therefore need to be small and hard. Seeds also need to have a coat which can withstand the effects of acids, enzymes and bacteria in the gut (Gardener *et al.* 1993a, b). Seeds that are permeable to water can swell, rupturing the seed coat and exposing the more degradable internal structures. A few species, however, seem to rely on this mechanism to break dormancy (Howe and Smallwood, 1982). Seed size and density can also affect the rate of passage through the gut, which determines the length of time they are exposed to digestive juices. Larger seeds of *Trifolium* spp. and some leguminous species have been found to pass through the gut more quickly in sheep and cattle (Russi *et al.*, 1992; Gardener *et al.*, 1993a).

Since seeds generally need to be small to survive passage through the gut, they are not likely to be attractive to herbivores as food in their own right. Although some species have palatable fruits or seed cases, many appear to increase the chance of being eaten by having leaves that are both palatable and close to the seed heads (Janzen, 1984; Middleton and Mason, 1992). Amongst grasses, for example, tussock-forming species with a tall seed head have been found to have poorer viability following digestion than lower growing, rhizomatous or stoloniferous grasses which have their seeds close to the leaves (Gardener *et al.*, 1993a).

Potentially, seeds attaching to coats may be dispersed further than those passing through the gut. Hooks or spurs on seeds enable them to be carried for longer than seeds without obvious means of attachment (Graae, 2000). In one study, as many as 8500 diaspores from 85 plant species were recovered during 16 examinations from the coat of one sheep, with seeds lasting up to 7 months (Fischer *et al.*, 1996). However, there do not appear to be any attempts to investigate this form of dispersal by deer, which have straighter hair and smoother coats than sheep.

Plants that are adapted to both epi- and endozoochorous dispersal occur in a wide range of taxonomic groups and environments, although they appear to be relatively common in scrub or woodland habitats, where wind and water may provide less power for dispersal. Furthermore, animals may act as a supplementary dispersal method for species which do not rely on them as their main dispersal agent (Vickery *et al.*, 1985; Malo and Suarez, 1998). Over 60 plant species that are known to occur in the British Isles have been identified from deer faecal pellets (Table 3).

Viability and dispersal rates

Although many seeds may be damaged during feeding or digestion, or suffer competition if they germinate in clusters from dung, seeds that remain viable following excretion have several advantages. They are supplied with nutrients and are protected from desiccation by dung pellets, and deposited in an environment which is likely to have been disturbed by browsing or trampling (Malo and Suarez, 1998). In Scottish heathland grazed by cattle, red deer and sheep, more graminoid seeds than those of dicotyledons were found to germinate from dung (Welch, 1985). Conversely, legume seeds are better than grass seeds at surviving in the digestive system of cattle (Gardener *et al.*, 1993a, b). However, both plant types showed pronounced variability, with legume seed survival varying from 0 to 78 per cent and grass seed survival from 0 to 64 per cent.

The number of seeds transmitted by dung varies considerably between herbivores, depending on their diets and digestive strategies, and may also depend on herbivore densities (Russi *et al.*, 1992; Middleton and Mason, 1992). Horses and pigs are considered less efficient than ruminants at producing viable seeds because they are more likely to crush seeds between their molars. Further, hindgut fermentation appears to delay the passage of seeds (Janzen *et al.*, 1985). Red deer have been estimated to pass 20 000 seeds per day in the Mediterranean *dehesa* (Malo and

Table 3: Plant species (present in the British Isles) which have been shown to germinate from dung of red (*Cervus elaphus*) and fallow (*Dama dama*) deer (Malo and Suarez, 1995; Welch, 1985)

Species	Fallow deer	Red deer	Species	Fallow deer	Red deer
Agrostis canina		*	*Medicago minima*	†	
Agrostis stolonifera	†		*Mentha pulegium*		†
Agrostis tenuis		*	*Mentha suaveolens*		†
Anthriscus caucalis		†	*Papaver rhoeas*	†	
Apera interrupta	†	†	*Papaver somniferum*		†
Aphanes microcarpa	†	†	*Plantago coronopus*	†	
Arenaria leptoclados	†	†	*Poa annua*	†	†/*
Calluna vulgaris		*	*Poa pratensis*		*
Capsella bursa-pastoris	†		*Polygonum hydropiper*	†	†
Cardamine hirsuta	†	†	*Polypogon monspeliensis*	†	†
Carex divisa		†	*Ranunculus parviflorus*	†	†
Centaurea melitensis		†	*Sagina apetala*	†	†
Cerastium glomeratum	†	†	*Sagina procumbens*		*
Cerastium semidecandrum	†	†	*Scirpus holoschoenus*		†
Epilobium tetragonum	†		*Sherardia arvensis*	†	
Erodium cicutarium	†		*Stellaria media*	†	†
Erodium moschatum	†		*Trifolium campestre*	†	†
Erophila verna		†	*Trifolium cernuum*	†	†
Filago pyramidata	†	†	*Trifolium scabrum*		†
Galium spurium	†	†	*Trifolium suffocatum*	†	†
Herniaria hirsuta		†	*Trifolium tomentosum*	†	†
Juncus articulatus		*	*Triticum aestivum*	†	†
Juncus acutiflorus	†	†	*Urtica urens*	†	†
Juncus bufonius	†	†/*	*Verbena officinalis*	†	
Juncus effusus		*	*Veronica arvensis*	†	†
Juncus inflexus	†	†	*Veronica verna*	†	
Juncus kochii		*	*Vulpia ciliata*	†	†
Juncus squarrosus		*	*Vulpia muralis*	†	†
Lolium rigidum	†	†			
Malva sylvestris	†				

* Welch, 1985; † Malo and Suarez, 1995.

Suarez, 1995), but this is less than the 300 000 estimated for cattle. Over the course of a year, an average of 735 seeds m^{-2} were estimated to be deposited by deer, cattle and rabbits in this eco-system (Malo *et al.*, 2000).

In view of the fact that deer move regularly between vegetation communities for foraging, both endo- and epizoochorous dispersal provides an important potential mechanism for coloniz-ation. Depending on the species and environment, deer may move distances of up to 10 km in the time they carry seeds, and they are more likely to distribute seeds evenly than birds, which tend to produce clusters near perching stations (Malo and Suarez, 1998). Seeds of *Cistus ladanifer*, for

example, have been found to be deposited by red deer in habitats hundreds of metres from their parent plants and a strain of *Mimulus guttatus* was recorded over 1 km away (Vickery *et al.*, 1985; Malo and Suarez, 1995).

Discussion

Deer clearly have a substantial impact on wood-land vegetation. By reducing height and growth of trees, shrubs and climbers, the biomass of understorey vegetation will be reduced, leading to a more open and simplified vertical structure. These changes are likely to have a significant

effect on woodland fauna. A wide range of woodland passerine species and some small mammals, for example, are dependent on understorey vegetation for foraging or nesting (Fuller and Henderson, 1992; Flowerdew and Ellwood, 2001; Fuller, 2001; Perrins and Overall, 2001).

It is also clear that deer change the species composition of young trees and shrubs in woodlands, tending to reduce diversity with increasing browsing pressure. In some cases, local extinction of vulnerable species may occur (Martin and Daufresne, 1999). Observations from enclosure studies suggest that while there are some species that are almost invariably depleted by deer, there are others that are depleted in some sites but increase in others. The effects of deer on vegetation are therefore not entirely consistent, but dependent on local ecological conditions. This suggests that while some aspects of the impact of deer on woodlands will be easy to predict, others will be variable and less certain. The conclusion that competition is important in affecting tree seedling survival, and that the strength of competition could be altered by the deer themselves is an important point. While it would be useful to assess the impact of deer in a range of conditions such as varying soil type or light regime, it is also important to understand the changes caused by deer as a process that is continually being affected by changing conditions.

In view of the lack of long-term data, an important question is whether these changes are likely to be permanent, or simply ephemeral due to changes associated with stand maturity. Attempts to model the effects of deer browsing on hemlock (*Tsuga canadensis*) forests, however, suggest that deer have a permanent effect on canopy composition (Frelich and Lorimer, 1985; Cornett *et al.*, 2000). Although long-term studies would clearly be useful, there are practical problems with continuing a study for several decades. The longest period of investigation so far published on the impacts of deer appears to be 33 years (Ross *et al.*, 1970; Risenhoover and Maass, 1987). However, in both study areas, the deer population changed substantially during the period and regular monitoring of both vegetation and deer populations was not always possible.

The effects of deer are clearly not confined to the direct effects of browsing within woodlands. The majority of woodlands in the lowlands of Britain are small (<1000 ha) and therefore exposed to deer carrying seeds from neighbouring agricultural habitats, and operations such as felling or coppicing will create ideal sites for colonization. Furthermore, the evidence available on seed dispersal by deer suggests that the majority of species that are likely to benefit include grasses, rushes and palatable herbs with small hard seeds. There are few records of seeds of shrubs and none of trees that occur in Britain. As a result, it appears that seed dispersal would be likely to strengthen the changes caused by browsing, namely to put trees and shrubs at a disadvantage with respect to grasses. However, few studies have focused on dispersal by deer and the dispersal mechanisms of many woodland plant species are poorly understood. A number of woodland species have very slow rates of dispersal and it is possible that large herbivores, now extinct, or even deer (which were rare until recently in the lowlands of Britain), were acting as dispersers for some of these species (Graae, 2000).

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